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The Reproductive Biology of the Paddlefish, Polyodon Spathula (Walbaum), in Lake Cumberland, Kentucky

John Hageman
Western Kentucky University

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1985

THE REPRODUCTIVE BIOLOGY OF THE PADDLEFISH, POLYODON
SPATHULA (WALBAUM), IN LAKE CUMBERLAND, KENTUCKY

A Thesis

Presented to

the Faculty of the Department of Biology

Western Kentucky University

Bowling Green, Kentucky

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

John Robert Hageman

March 1985

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THE REPRODUCTIVE BIOLOGY OF THE PADDLEFISH, POLYODON
SPATHULA (WALBAUM), IN LAKE CUMBERLAND, KENTUCKY

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THE REPRODUCTIVE BIOLOGY OF THE PADDLEFISH (POLYODON
SPATHULA) IN LAKE CUMBERLAND, KENTUCKY

John Robert Hageman March 1985

66 pages

Directed by: R. Hoyt, B. Ferrell, and G. Dillard

Department of Biology

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The reproductive biology of the paddlefish (Polyodon spathula) was studied on specimens collected from Lake Cumberland, Kentucky, from September 1983 to July 1984. A total of 500 specimens was studied. Reproductive activity was observed on 17 April 1984 in the Big South Fork of Lake Cumberland. Seasonal differences were observed in sex ratios with more males than females occurring in the winter and spring. Movements were observed throughout the year, but these were accentuated prior to reproduction in the spring. Lake Cumberland paddlefish became sexually mature by Age Group V in males and VIII in females. In the spring, gravid females were found only in upstream spawning areas while non-gravid females occurred throughout the rest of the lake. This supported the alternating year spawning hypothesis for females of this species; mature males were found in all lake locations sampled at this time. Gonad development in Lake Cumberland paddlefish started in September-October and continued progressively throughout the

year until egg release. Gonad fat bodies responded inversely with gonad development, progressively decreasing in size as the gonads increased. The liver and throat fat bodies did not show this weight correlation but were concluded to be important in the energetics of the gonads. Coefficients of condition for Lake Cumberland paddlefish corresponded closely with gonad development. Condition values for Lake Cumberland paddlefish were greater than those reported in the literature. This supported the idea that the optimum habitat for paddlefish is in lakes rather than rivers. The estimated average annual fecundity for Lake Cumberland paddlefish was similar to that reported in other studies. No relationship was seen between number of eggs and fish size. All sexually mature males and some females exhibited prominent secondary sexual characteristics.

INTRODUCTION

The family Polydontidae consists of only two extant species: Psephurus gladius (Martens) in the Yangtze River system in China and Polyodon spathula (Walbaum), commonly referred to as the paddlefish, in the Mississippi River drainage system of North America. At present, paddlefish are widely distributed and reported to extend into 22 states (Carlson and Bonislowsky 1981). Much work has been done on the biology of the paddlefish, and a bibliography on the species has been prepared by Graham and Bonislowsky (1978). Carlson and Bonislowsky (1981) provided an excellent review of the literature on the fishery of the species.

An increased demand for paddlefish at both the commercial and sports level, in conjunction with the fear of the possible disruption of its breeding habitat by dam construction, has stimulated renewed interest in the life history of the paddlefish. The success of artificial propagation experiments by Meyer and Stevenson (1962), Purkett (1963a), Ballard and Needham (1964), Needham (1965), Friberg (1972), Russell (1973), and Kallemeyn (1974) have made the species a potentially manageable resource. Consequently, many states having exploitable paddlefish populations within their borders have made a directed effort to identify and describe that resource.

Lake Cumberland, Kentucky, provides a unique setting for the study of the biology of the paddlefish. The paddlefish population represents a closed gene pool, being separated from Cumberland River fish below the lake by the Wolf Creek Dam and not influenced by genetic input from upstream populations due to the headwater nature of the tributary streams.

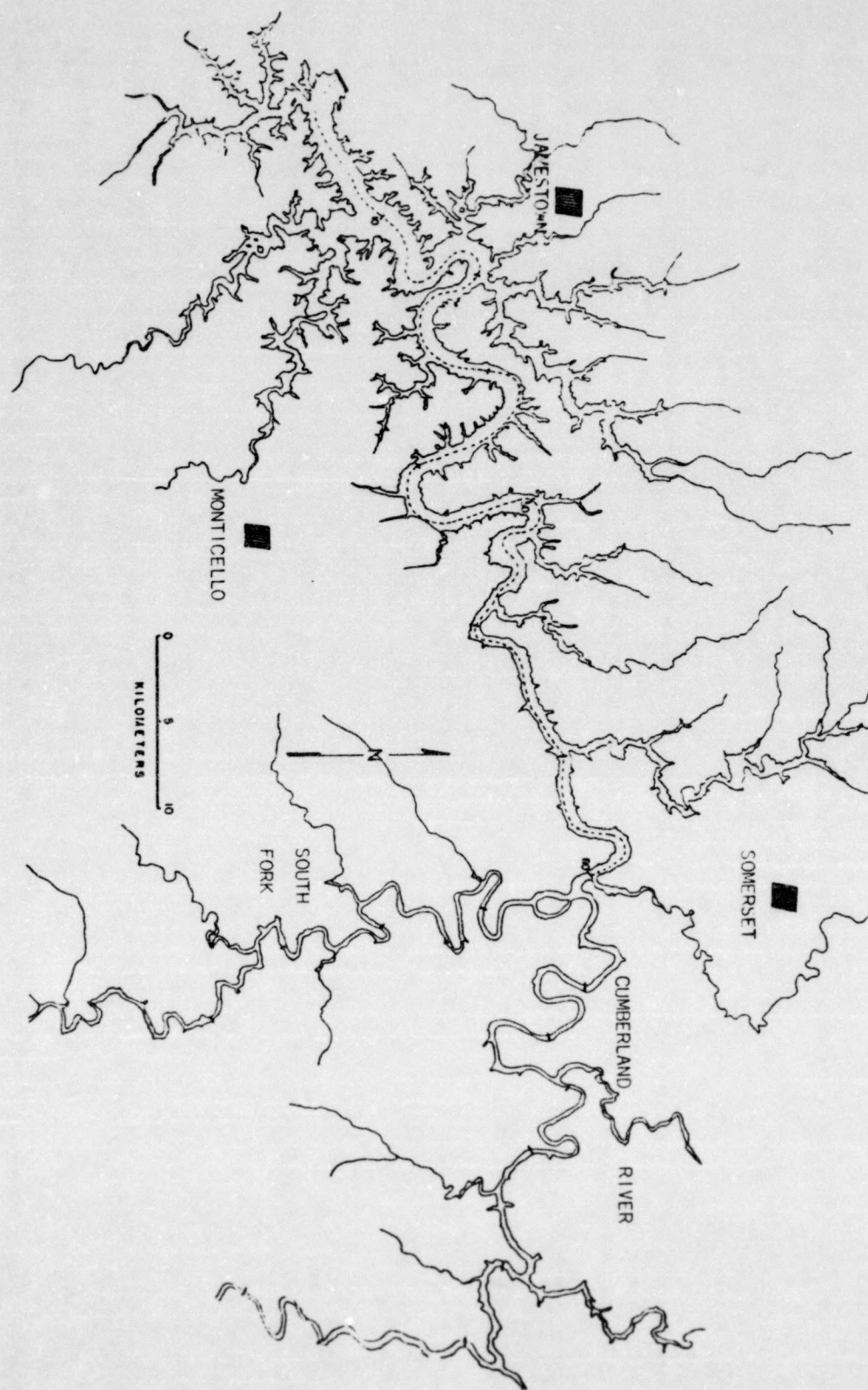
The objective of this study was to describe the reproductive biology of the paddlefish in Lake Cumberland through an annual cycle.

STUDY AREA

Lake Cumberland is an upstream impoundment on the Cumberland River in southeastern Kentucky (Figure 1). The lake and its two major tributaries, the Big South Fork and the Cumberland River, are bordered by Russell, Pulaski, McCreary, Wayne, and Clinton counties. The lake is a Corps of Engineers multipurpose impoundment formed in 1951 with the completion of the Wolf Creek Dam across the Cumberland River. The lake has a drainage area of 15,046 square kilometers and an average depth of 27.5 meters; it is over 161 kilometers long with more than 1,700 kilometers of shoreline. It has a surface area of 20,336 square kilometers at a summer pool depth of 220.5 meters above mean sea level (Henley 1967).

The watershed lies in the Highland Rim and Cumberland Plateau Physiographic Regions. The substrate is composed of a rock structure that gives rise to relatively unproductive soil. Major vegetation is that indigenous to the mixed mesophytic forest with areas of sparse pasture land and some small-plot plow cultivation. The most immediate watershed is deep narrow valleys and steep wooded hillsides. All of this contributes to low mineral nutrient levels washing into the lake.

Figure 1. Map of Lake Cumberland, Kentucky, and its tributaries, the Big South Fork and Cumberland River.



PHYSICO-CHEMICAL LAKE CONDITIONS

Weekly water temperature and lake level readings for Lake Cumberland for the duration of the study were provided by the Nashville district office of the U. S. Army Corps of Engineers (Figures 2 and 3, respectively). Temperatures were recorded at Burnside at the confluence of the Cumberland River and the Big South Fork. Temperature readings were taken at the surface and 7.62 meters. Lake level readings were made at the Wolf Creek Dam.

Dissolved oxygen concentration and water temperatures were recorded on each collecting trip (Table 1).

Figure 2. Mean weekly water temperatures at the surface and 7.6 m at Lake Cumberland, Kentucky, September 1983 to August 1984.

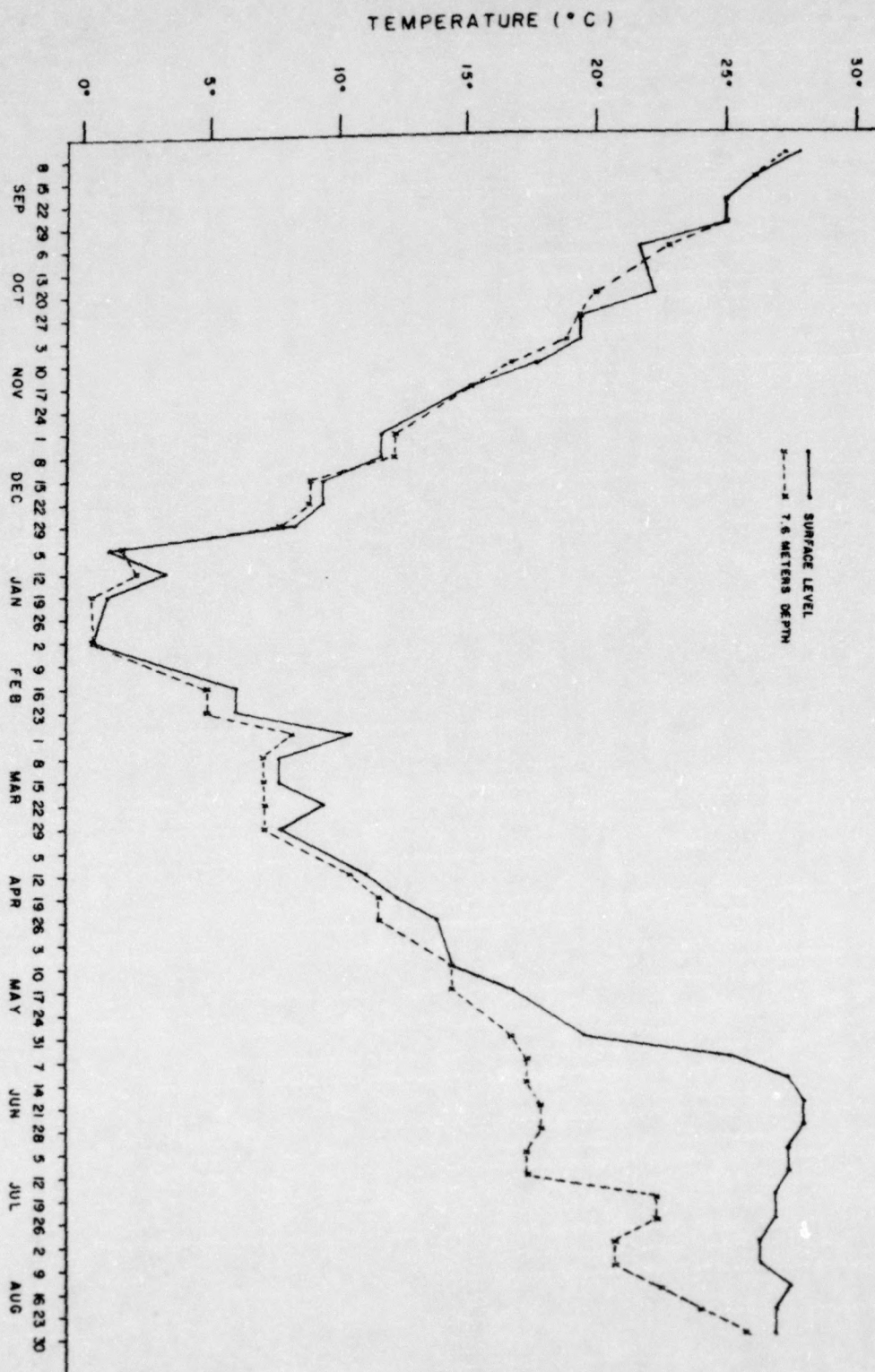


Figure 3. Lake level in meters above mean sea level at Lake Cumberland, Kentucky, September 1983 to August 1984.

LAKE LEVEL IN METERS ABOVE MEAN SEA LEVEL

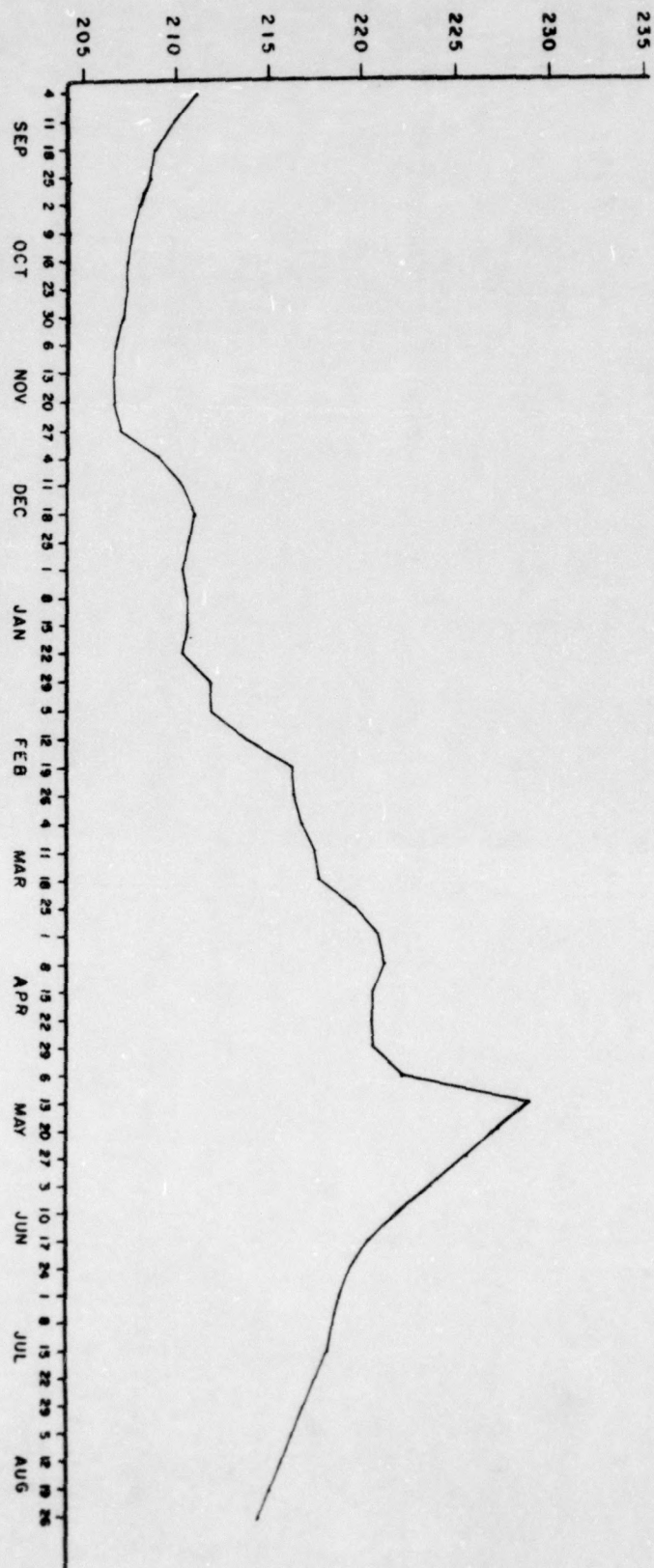


Table 1. Temperature (C) and Dissolved Oxygen (mg/l), in Lake Cumberland, Kentucky, September 1983 to June 1984.

DATES	SURFACE	5 METERS	10 METERS	14 METERS
16-18 Sept.				
Temp.	26.0	25.0	25.0	25.2
D.O.	--	--	--	--
30 Sept.-2 Oct.				
Temp.	22.0	22.1	22.1	18.5
D.O.	9.2	9.3	9.4	2.0
28-30 Oct.				
Temp.	15.1	16.2	15.3	15.2
D.O.	10.1	10.6	7.4	6.6
2-4 Dec.				
Temp.	11.0	--	10.0	11.0
D.O.	11.5	--	11.2	10.8
17-19 Dec.				
Temp.	5.0	5.0	6.0	6.0
D.O.	12.0	12.1	12.4	11.7
5-7 Jan.				
Temp.	4.0	4.0	4.0	4.0
D.O.	10.4	10.2	9.0	8.8
17-19 Feb.				
Temp.	7.5	7.8	6.7	6.0
D.O.	11.7	12.0	11.8	11.5
2-4 Mar.				
Temp.	13.8	15.5	14.0	11.8
D.O.	1.3	1.5	2.0	2.0
16-18 Mar.				
Temp.	6.0	4.9	4.0	4.0
D.O.	12.6	11.8	11.9	11.9
6-8 Apr.				
Temp.	8.5	8.0	7.9	7.8
D.O.	11.8	12.4	11.2	10.6
27-28 Apr.				
Temp.	16.0	14.0	13.6	13.0
D.O.	9.2	9.4	8.8	8.6
21-22 May				
Temp.	19.5	16.0	13.5	12.0
D.O.	8.5	5.2	4.1	3.8

METHODS and MATERIALS

Paddlefish were collected from Lake Cumberland and its major tributaries on twelve collecting trips from September 1983 to May 1984. Trips were made twice a month during October, December, March, and April and once a month during September, January, February, and May (Table 2). This collecting schedule was determined by mortality rates of the paddlefish in the tackle, weather conditions, and lake water levels.

The trips on 30 September, 2 December, and 5 January were made to the main body of the lake, the 16 September, 17 December, 17 February, 27 April, and 21 May collections were on the Big South Fork, and the 28 October, 2 March, 16 March, and the 6 April collections were made on the Cumberland River. Generally, collecting trips began on Friday and lasted to Sunday giving the nets a forty-eight hour sampling time. Each net was 91 m long and 5 m deep (hobbled to 4 m) with a bar mesh size of 12.7 or 15.24 cm. On lake collections, one or two nets were set with one end anchored on the shore and extended perpendicularly out in the water. There were never more than two nets tied together. When upper river and tributary collections were

Table 2. Schedule of collecting trips to Lake Cumberland, Kentucky, September 1983 to July 1984.

TRIP	DATE	LOCATION
1	Sept. 16-18	S.F.-Garnett Bend
2	Sept. 30-Oct 2	M.L.-Fall Creek Ramp
3	Oct. 28-30	C.R.-Cave Creek
4	Dec. 2- 4	M.L.-Waitsboro
5	Dec. 17-19	S.F.-Turkey Creek
6	Jan. 5- 7	M.L.-Fall Creek Ramp
7	Feb. 17-19	S.F.-Turkey Creek
8	Mar. 2- 4	C.R.-Sawyer Ramp
9	Mar. 16-18	C.R.-Cave Creek
10	Apr. 6- 8	C.R.-Cave Creek
11	Apr. 27-28	S.F.-Alum Ford
12	May 21-22	S.F.-Alum Ford

C.R. = Cumberland River

M.L. = Main Lake

S.F. = Big South Fork

made the net or nets were stretched from bank to bank. All sets were made over the old river channel. The location and depth for tackle sets were determined just prior to each trip by conversations with local commercial fishermen. Under normal sampling conditions, twelve nets were set per collecting trip. The frequency of checking nets was determined by the success of capture as well as water level, weather, and boat traffic conditions.

All fish caught alive were identified, weighed, measured, and released. Paddlefish were tagged as part of the study. Dead paddlefish were weighed and measured, the lower jaw removed, and the total body cavity contents removed and fixed in 10% formalin.

Data sets were also purchased from local commercial fishermen. A data set consisted of all viscera, the location of capture, total body weight, total body length (TL), eye-fork length (EFL), and the lower jaw from paddlefish collected on lake Cumberland and its tributaries. The total length was measured from the anterior tip of the rostrum to the dorsal tip of the caudal fin; the eye-fork length was the distance from the eye to the fork in the tail. These data were placed in plastic bags with the viscera which were frozen in monthly lots for later work-up in the laboratory. Approximately forty-five data sets were provided for each month of the study.

In the laboratory specimen analysis involved identifying the gonads as to right and left organs and separating the gonads from their accompanying fat bodies and

weighing each to the nearest gram. The liver was removed and weighed. The measure of throat fat was determined by excising and weighing the portion of the foregut between the anterior edge of the stomach rugae and the posterior edge of the esophageal papillae.

Fecundity was determined for females in the following manner. Roe from gravid females caught by commercial fisherman was weighed as eggs and fat bodies together and reported as roe weight. The roe was processed and sold as caviar by commercial fishermen; estimations were made to determine fat body to egg ratios. Gravid females obtained from collecting trips were analyzed by separating the fat bodies from the eggs on both left and right sides and weighing each separately. Subsampling of approximately 5% by weight was used to determine the total number of eggs on each side. Egg diameters were measured with a millimeter ruler.

The age of fish was determined by cross-sectioning the dentary bone and counting the annuli according to Adams (1942).

Statistical analyses were applied to age, sex, month of capture, and location of capture. Statistics applied included mean, range, standard deviation, and standard error of the mean.

The Gonosomatic Index (GSI), Fat Body Index (FBI), Hepatosomatic Index (HSI), Throat Fat Index (TFI), and Coefficient of Condition (K) for eye-fork length and total length were determined using the equations

$$\text{GSI} = \frac{\text{total gonad weight}}{\text{total body weight}} * 100$$

$$\text{FBI} = \frac{\text{total fat body weight}}{\text{total body weight}} * 100$$

$$\text{HSI} = \frac{\text{liver weight}}{\text{total body weight}} * 100$$

$$\text{TFI} = \frac{\text{throat fat weight}}{\text{total body weight}} * 1000$$

$$\text{K}_{\text{EFL}} = \frac{\text{body weight} * 10^5}{\text{eye-fork length}^3}$$

$$\text{K}_{\text{TL}} = \frac{\text{body weight} * 10^5}{\text{total length}^3}$$

(weight in grams and length in millimeters)

RESULTS

A total of 500 paddlefish was used in the study, 469 provided by contracted commercial fishermen and 31 mortalities from the lake collections. Male paddlefish averaged less in total body weight and total body length than females, 10.7 kg vs. 15.4 kg and 133 cm vs. 142 cm, respectively (Table 3). Males likewise were younger than females, averaging 5.4 years of age, ranging from 2 to 9; females averaged 6.8 years, ranging from 2 to 14 (Table 4 ; Figure 4). The majority of paddlefish studied was collected from the uplake tributaries, 225 from the Cumberland River, 136 from the Big South Fork, and 23 from Lake Cumberland. A total of 116 specimens did not have location of capture information.

Sex Ratios - Significantly more males were observed in the study than females, 305 vs. 195 ($P < 0.05$) (Table 5). Sex ratios varied seasonally with significantly more males than females occurring in the winter (118 vs. 35) and spring (92 vs. 61) and more equal numbers in the fall (79 and 71) and summer (16 and 28). Females outnumbered males only during the summer (Table 5).

Sexual Maturity - Based upon gonad development (GSI values), sexual maturity was observed to occur in males earlier than

Table 3. Mean total length in cm and body weight in kg of paddlefish from Lake Cumberland, Kentucky, September 1983 to July 1984.

	MALES			FEMALES		
	Lgth.	Wt.	N	Lgth.	Wt.	N

September	130	9.3	(28)	136	11.9	(21)
October	127	8.2	(19)	138	12.4	(32)
November	135	11.7	(32)	150	20.0	(18)
December	134	11.3	(49)	103	18.2	(11)
January	133	11.1	(33)	144	15.0	(13)
February	134	10.8	(36)	148	17.5	(11)
March	136	11.0	(32)	144	14.3	(12)
April	129	11.0	(47)	150	19.7	(15)
May	136	9.4	(13)	149	15.7	(34)
June	134	11.1	(14)	142	14.7	(26)
July	135	12.7	(2)	138	13.8	(2)
AVERAGE	133	10.7	(305)	142	15.4	(195)

Table 4. Age groups of paddlefish from Lake Cumberland
Kentucky, September 1983 to July 1984.

AGE GROUP	TOTAL N	
	MALES	FEMALES

I	0	0
II	2	3
III	7	5
IV	24	15
V	132	28
VI	104	45
VII	21	18
VIII	4	31
IX	1	37
X	0	8
XI	0	1
XII	0	1
XIII	0	0
XIV	0	1

Figure 4. Mean age of paddlefish collected from Lake Cumberland, Kentucky, September 1983 to July 1984.

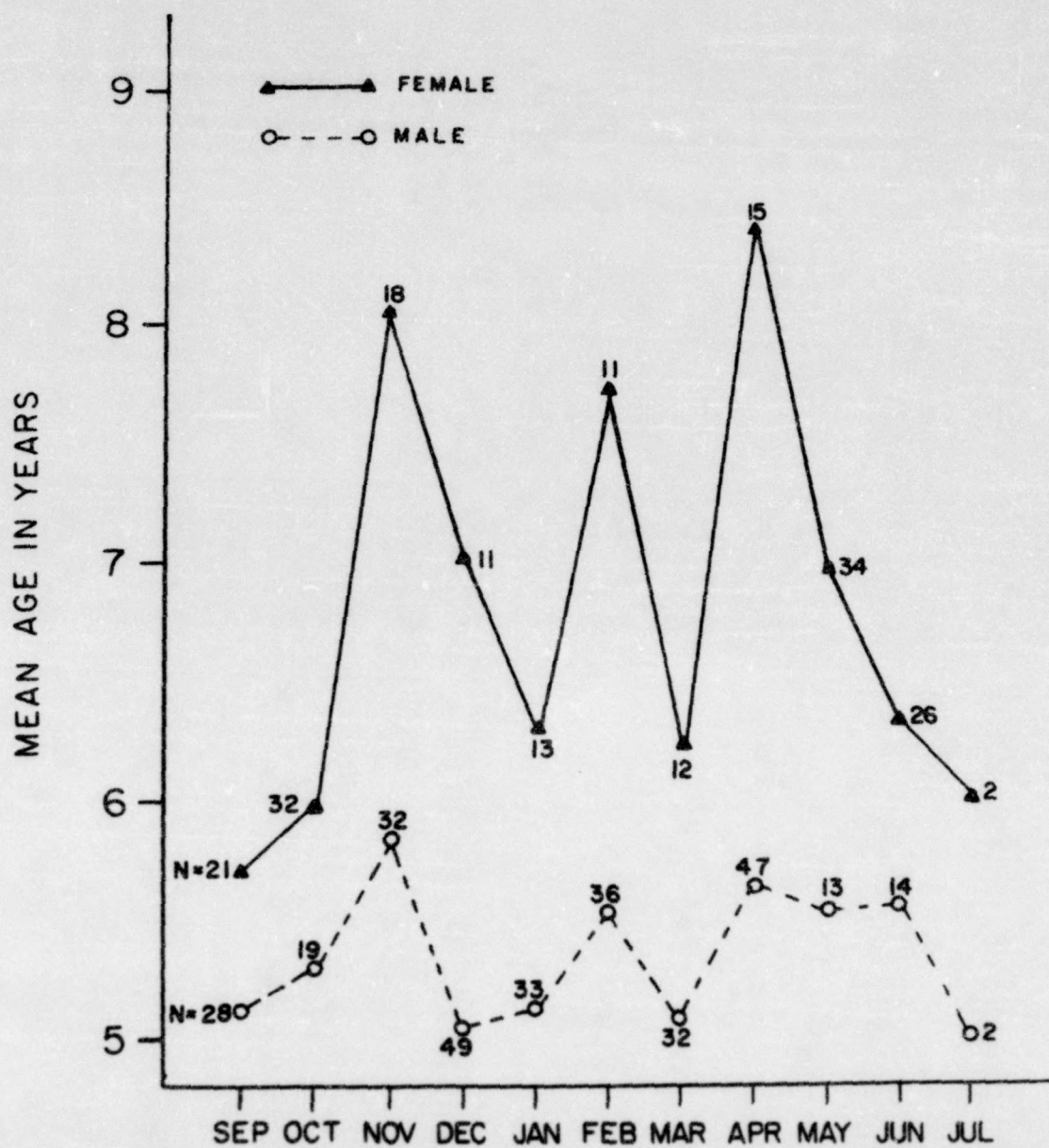


Table 5. Sex ratio, Chi-square and significance for paddlefish from Lake Cumberland, Kentucky, September 1983 to August 1984.

MONTH & SEASON	MALES	FEMALES	CHI-SQUARE	SIGNIFICANCE
September	28	21		
October	19	32		
November	32	18		
FALL	79	71	0.529	0.3 - 0.5
December	49	11		
January	33	13		
February	36	11		
WINTER	118	35	45.02	< 0.001
March	32	12		
April	47	15		
May	13	34		
SPRING	92	61	6.28	0.01 - 0.02
June	14	26		
July	2	2		
August	0	0		
SUMMER	16	28	3.28	0.05 - 0.1
SUB-TOTAL	305	195	24.50	< 0.001
TOTAL	500			

females (Table 6). Males reached sexual maturity by Age Group V with mean GSI values of 0.65, whereas most females did not mature until Age Group VIII with mean GSI values of 5.0.

Gonad Weights - Female gonad weights averaged much greater than those of males throughout the entire study, 680.0 g vs. 58.4 g, respectively. The left gonad averaged more in weight than the right in both sexes, 194 vs. 186 g, respectively, for females and 31 vs. 27 g, respectively, for males (Table 7). Maximum average gonad weights of males were observed in November and December progressively decreasing throughout the remaining months. Female gonad weights were greatest in April with no annual or seasonal trend.

Gonosomatic Indices - Gonosomatic indices showed seasonal trends similar to the gonad weight values (Figures 5 and 6). Average GSIs for males reached a maximum of 0.9 in November and progressively declined to a mean monthly minimum of 0.1 in July. Female GSI values were greatest in April (7.8) and lowest in July (0.8). However, while male GSI values showed a progressive increase female values fluctuated through time (Figures 5 and 6). Mean GSI values showed marked increases during different stages in the life cycle for males and females increasing from 0.06 to 0.69 from Age Groups III to V in males and from 0.9 to 5.2 from Age Groups VI to VIII in females (Table 6).

Fish taken from Lake Cumberland had lower mean GSI values than fish taken from the Big South Fork and

Table 6. Gonosomatic Indices by age group for paddlefish
from Lake Cumberland, Kentucky, September 1983 to July 1984.

AGE GROUP	GSI	
	MALES	FEMALES
I	--	--
II	0.07	0.12
III	0.06	0.25
IV	0.37	0.34
V	0.69	0.54
VI	0.66	0.96
VII	0.71	3.17
VIII	0.57	5.20
IX	0.32	5.95
X	--	6.47
XI	--	9.14
XII	--	1.50
XIII	--	--
XIV	--	0.18

Table 7. Gonad weights in grams for paddlefish from Lake Cumberland, Kentucky, September 1983 to July 1984.

	MALES				FEMALES				
	LEFT	RIGHT	TOTAL	N	LEFT	RIGHT	N	TOTAL	N
Sept.	10.46	8.40	18.86	(25)	192.55	160.25	(21)	352.80	(21)
Oct.	19.21	21.32	40.53	(19)	188.13	173.70	(30)	416.61	(32)
Nov.	58.41	47.69	106.10	(29)	75.50	59.00	(2)	1211.19	(17)
Dec.	50.71	44.02	94.73	(41)	27.50	31.75	(4)	986.02	(11)
Jan.	42.61	37.88	80.49	(33)	28.12	29.50	(8)	626.53	(13)
Feb.	45.11	37.00	82.11	(35)	332.00	464.00	(3)	1305.73	(11)
Mar.	42.47	37.41	79.88	(32)	41.71	39.36	(7)	593.50	(12)
Apr.	41.11	33.94	75.05	(47)	1028.50	920.75	(4)	1596.45	(15)
May	22.38	16.77	39.15	(13)	78.61	69.91	(33)	148.52	(33)
June	6.79	6.50	13.29	(14)	76.69	63.58	(26)	140.27	(26)
July	7.50	4.50	12.00	(2)	69.00	39.00	(2)	108.00	(2)
TOTAL	346.76	295.43	642.19	(290)	2138.31	2050.80	(140)	7486.6	(193)
AVERAGE	31.52	26.85			194.39	186.43			

Figure 5. Mean monthly Gonosomatic Indices from paddlefish collected for Lake Cumberland, Kentucky, September 1983 to July 1984.

Gonosomatic Index = G.S.I.

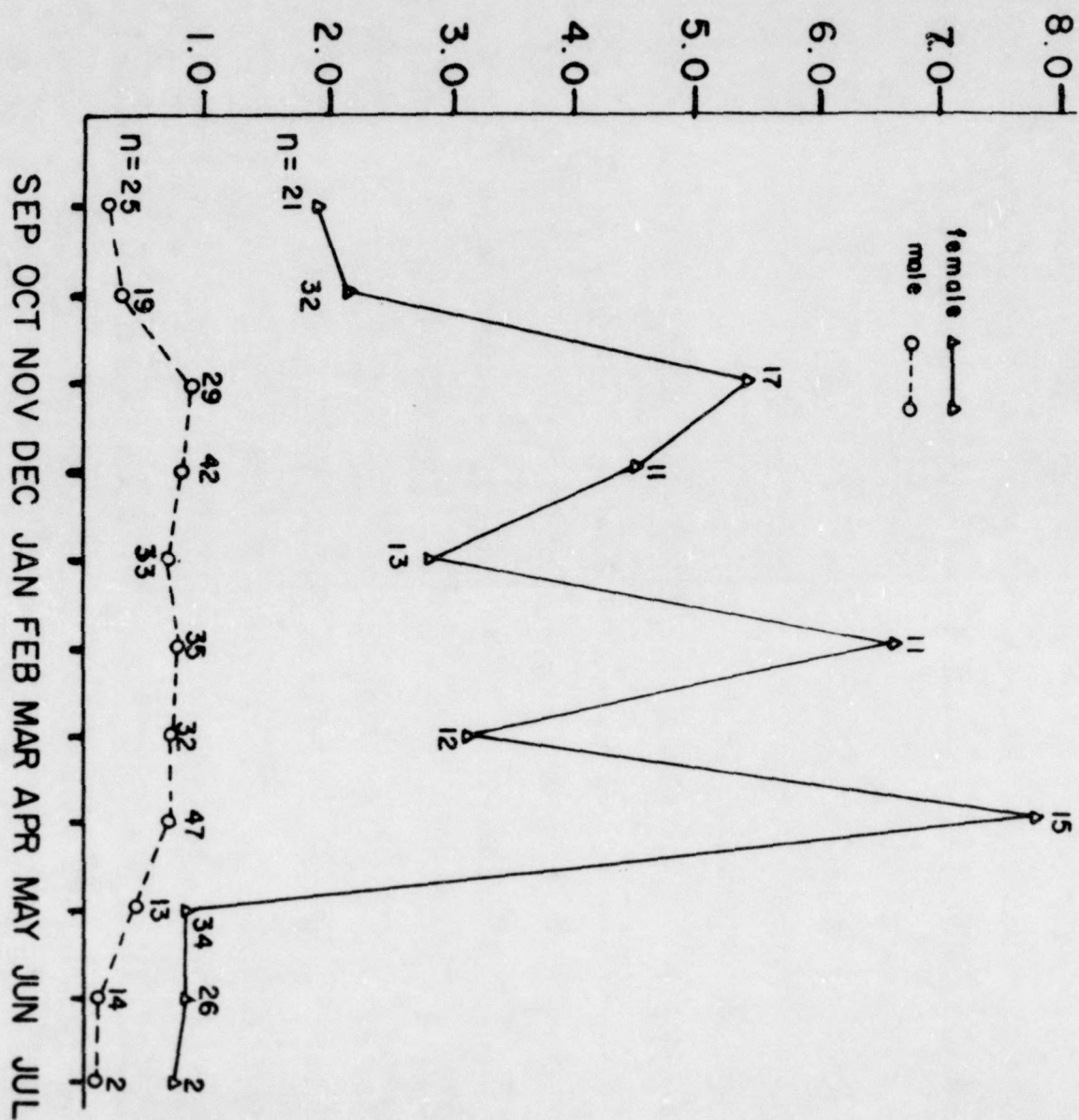
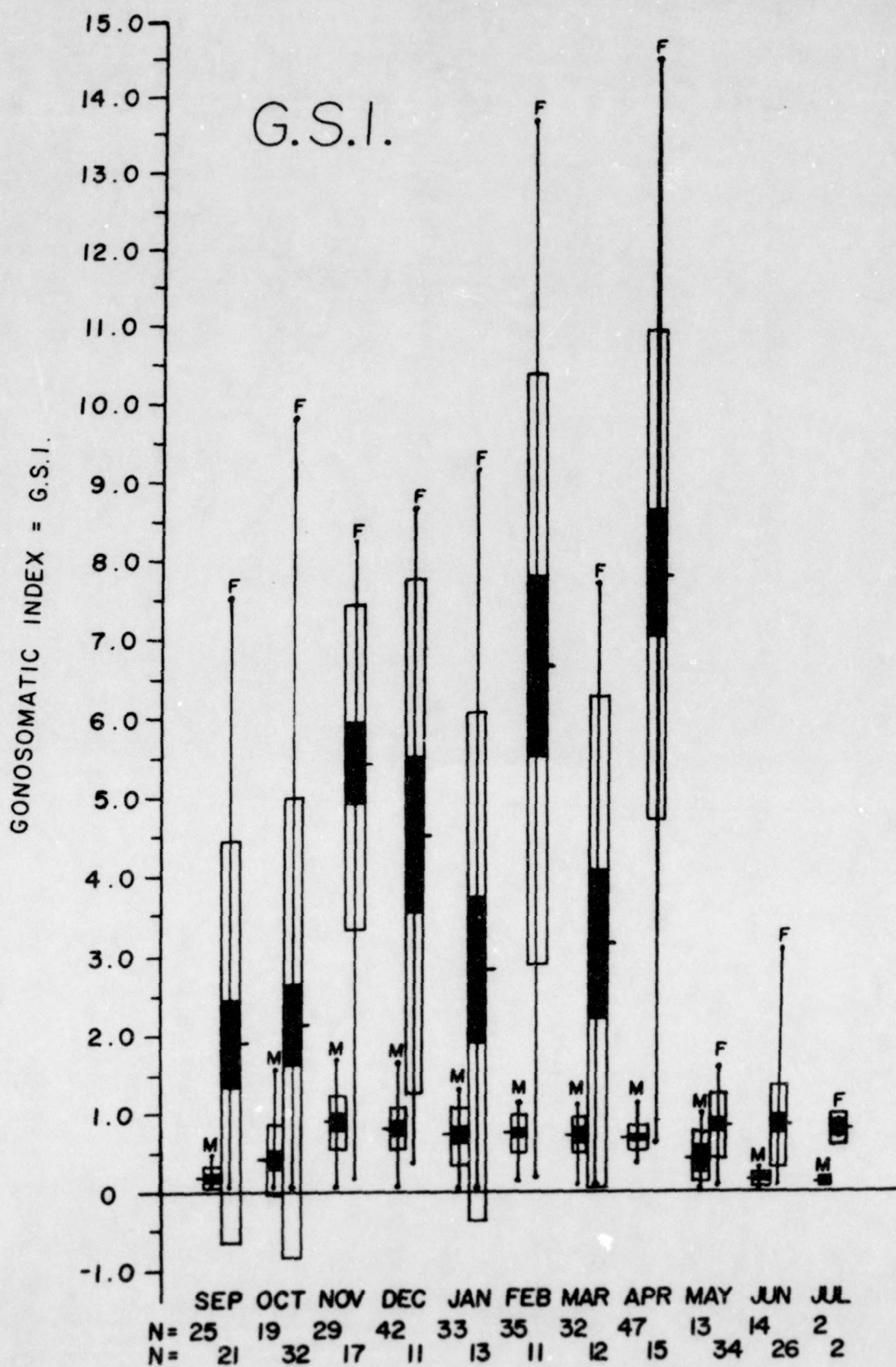


Figure 6. Monthly Gonosomatic Indices, means, standard deviations, standard error of the mean, and ranges for paddlefish collected from Lake Cumberland, Kentucky, September 1983 to July 1984.



Cumberland River, 0.61, 0.66, and 0.69, respectively, for males and 1.34, 3.07, and 3.35, respectively, for females.

Mature female GSI values increased monthly prior to the spawn and declined in May at all three study locations. The fish from the Big South Fork had higher GSIs in December through April.

Mature males showed little difference in gonad development from September through April at all three study locations with mean GSIs ranging from 0.71 to 0.94 with an overall average of 0.77. This decreased to a monthly average of 0.24 in May, June, and July. Immature males showed no observable trend (Table 8).

Fecundity - Five gravid females were taken in the study, one each in October and February, and three in April. These egg bearing specimens had a mean total body weight of 20.8 kg and an average total body length of 142.2 cm. Estimated egg counts ranged from 186,266 in an April fish to 252,386 in an October fish. No correlation was observed between fish body size and number of eggs present (Table 9).

Mean ova diameters ranged from 2.0 mm in an October fish to 3.0 mm in two April fish. Ova diameters appeared to be closely correlated with season. The percentage of ovary weight represented by egg weights ranged from 74 percent in October to 99 percent in February (Table 9).

Coefficient of Condition - Both eye-fork length and total body length condition values were calculated (Table 10), and both showed similar annual trends. The average K for females was slightly greater than that for males, 1.58 and ^{EFL}

Table 8. Gonosomatic indices by age group, sex, location, and season for paddlefish collected from Lake Cumberland, Kentucky, September 1983 to July 1984.

		Age	Sept	Oct	Nov	Dec	Jan	Feb	March	April	May	June	July
Main Lake													
Male	1-4	----				0.04	(2)		----			----	
Male	5-9	----				0.73	(9)		----			----	
Female	1-6		0.51	(2)		0.31	(1)		----			----	
Female	7-14		0.96	(3)		*2.62	(3)		----			----	
Big South Fork													
Male	1-4	----				0.24	(4)		0.67	(1)		0.43	(2)
Male	5-9		0.85	(16)		0.86	(26)		0.71	(17)		0.24	(16)
Female	1-6		1.45	(1)		2.42	(3)		----			0.66	(17)
Female	7-14		*5.83	(9)		*7.10	(5)		*9.67	(4)		1.16	(14)
Cumberland River													
Male	1-4	----				0.39	(7)		0.37	(4)		0.65	(1)
Male	5-9		0.94	(12)		0.76	(56)		0.71	(54)		0.23	(10)
Female	1-6		0.13	(1)		0.44	(8)		0.67	(8)		0.71	(20)
Female	7-14		*5.92	(6)		*6.99	(13)		*7.91	(14)		1.06	(8)

(* Include fish with roe taken by commercial fishermen)

Table 9. Mean ova diameter and percent of egg weight to roe weight for paddlefish from Lake Cumberland, Kentucky, September 1983 to July 1984.

MONTH	BODY WT.	% EGGS	# of EGGS	EGG DIAMETER	AGE
<hr/>					
October	24.041 k	84.40%	252,386	2.0 mm	8
February	17.237 k	99.08%	194,532	2.7 mm	7
April	19.845 k	91.82%	189,299	3.0 mm	8
April	20.639 k	98.23%	311,450	3.0 mm	9
April	22.680 k	87.40%	186,266	2.8 mm	9

Table 10. Coefficients of Condition - EFL and TL, for paddlefish collected with net tackle and commercial snag lines from Lake Cumberland, Kentucky, September 1983 to July 1984.

	MALES					FEMALES				
	TOTAL		COMMERCIAL			TOTAL		COMMERCIAL		
	TL	N	TL	EFL	N	TL	N	TL	EFL	N
September	0.418	(28)	0.419	1.562	(26)	0.433	(21)	0.427	1.493	(19)
October	0.386	(19)	0.382	1.442	(17)	0.435	(32)	0.417	1.492	(30)
November	0.472	(32)	0.472	1.640	(32)	0.563	(18)	0.563	1.700	(18)
December	0.465	(49)	0.463	1.534	(46)	0.488	(11)	0.489	1.569	(11)
January	0.423	(33)	0.430	1.519	(33)	0.451	(13)	0.458	1.555	(12)
February	0.442	(36)	0.444	1.511	(35)	0.512	(11)	0.516	1.726	(10)
March	0.433	(32)	0.434	1.491	(32)	0.444	(12)	0.444	1.558	(12)
April	0.568	(47)	0.428	1.514	(33)	0.625	(12)	0.521	1.601	(12)
May	0.367	(13)	0.367	1.297	(13)	0.458	(34)	0.457	1.568	(34)
June	0.450	(14)	0.450	1.702	(14)	0.469	(26)	0.469	1.698	(26)
July	0.522	(2)	0.522	1.890	(2)	0.529	(2)	0.529	1.543	(2)
AVERAGE	0.457	(305)	0.437	1.531	(283)	0.480	(195)	0.469	1.588	(186)

1.53, respectively. The monthly K_{EFL} values for males fluctuated little through the year with the lowest average value being observed in May (1.39) and the highest in July (1.89). Female "K" values showed no pattern and fluctuated throughout the year (Table 10).

Gonad Fat Bodies and Fat Body Index (FBI)- The mean weight of gonad fat bodies was 519 g for males and 377 g for females. The left gonad fat body in both sexes weighed more than the corresponding right body, 277 vs. 242 g, respectively, for males, and 193 vs. 153 g, respectively, for females (Table 11).

The average gonad Fat Body Index for the entire study was 4.64 for males and 3.99 for females. The highest average monthly FBI values were 5.40 for males in November and 4.66 for females in June. The lowest monthly average value for both males and females was observed in October, 2.77 for the males and 0.83 for the females (Figures 7 and 8).

Liver and Hepatosomatic Index (HSI) - Liver weights from 265 males averaged 142 g while those from 155 females averaged 209 g. These weights represented mean HSI values of 1.32 and 1.46 for males and females, respectively. High mean monthly HSI values were observed for males in June, 1.98, and for females in May, 2.09. The low mean monthly value for both sexes was observed in July, 0.98 and 0.86 for males and females, respectively (Figures 9 and 10).

Throat Fat and Throat Fat Index (TFI) - Throat fat weights averaged 20 g for 265 males and 33 g for 155 females; TFI

Table 11. Mean monthly gonad fat body weights for paddlefish from Lake Cumberland, Kentucky, September 1983 to July 1984.

	MALE				FEMALE			
	LEFT	RIGHT	N	TOTAL N	LEFT	RIGHT	N	TOTAL N
September	246	212	(25)	458 (25)	185	160	(21)	345 (21)
October	136	124	(19)	260 (19)	194	148	(30)	343 (32)
November	363	301	(29)	664 (29)	193	158	(2)	302 (17)
December	322	283	(41)	605 (41)	104	75	(4)	337 (11)
January	293	243	(33)	536 (33)	98	73	(8)	281 (13)
February	306	258	(35)	564 (35)	24	20	(3)	280 (11)
March	308	260	(32)	568 (32)	173	130	(7)	273 (12)
April	275	234	(47)	509 (47)	108	131	(4)	151 (15)
May	191	161	(13)	352 (13)	357	273	(33)	630 (33)
June	275	243	(14)	518 (14)	509	345	(26)	854 (26)
July	337	339	(2)	676 (2)	182	175	(2)	356 (2)
AVERAGE	277	242	(290)	519 (290)	193	153	(140)	377 (193)

Figure 7. Mean monthly Fat Body Indices for male and female paddlefish collected from Lake Cumberland, Kentucky, September 1983 to 1984.

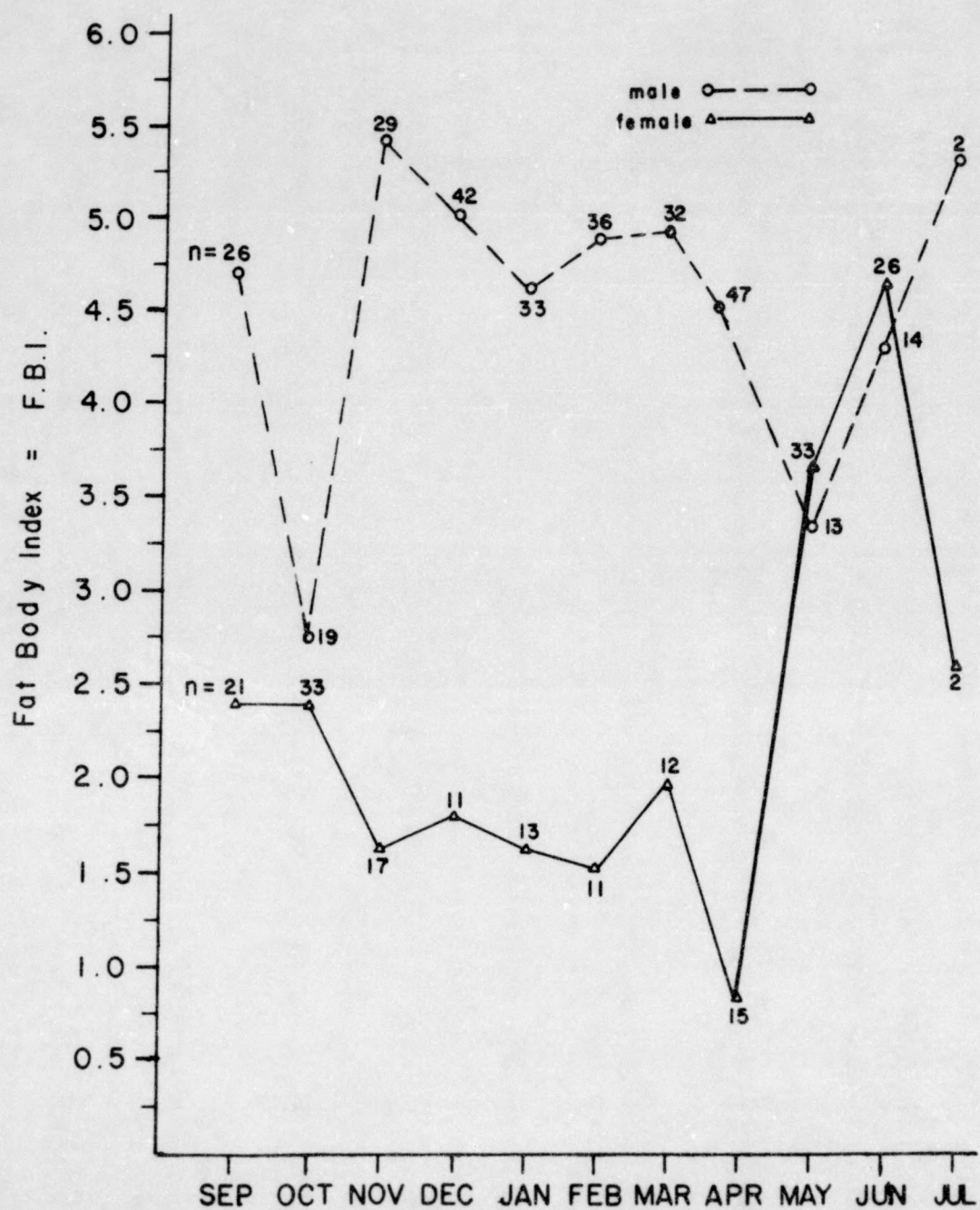


Figure 8. Monthly Fat Body Indices, means, standard deviations, standard error of the mean, and ranges for paddlefish collected from Lake Cumberland, Kentucky, September 1983 to July 1984.

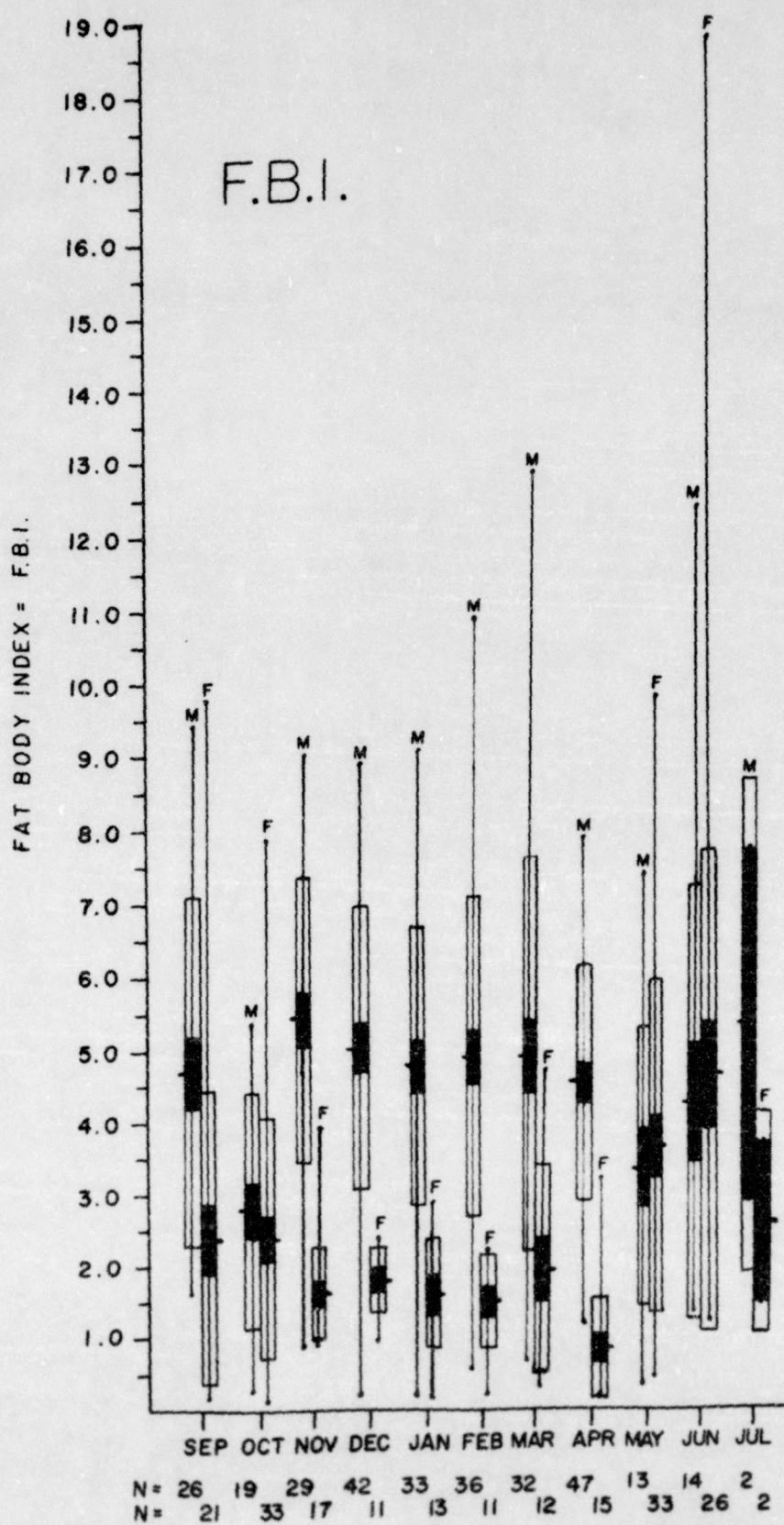


Figure 9. Mean monthly Hepatosomatic Indices for paddlefish collected from Lake Cumberland, Kentucky, September 1983 to 1984.

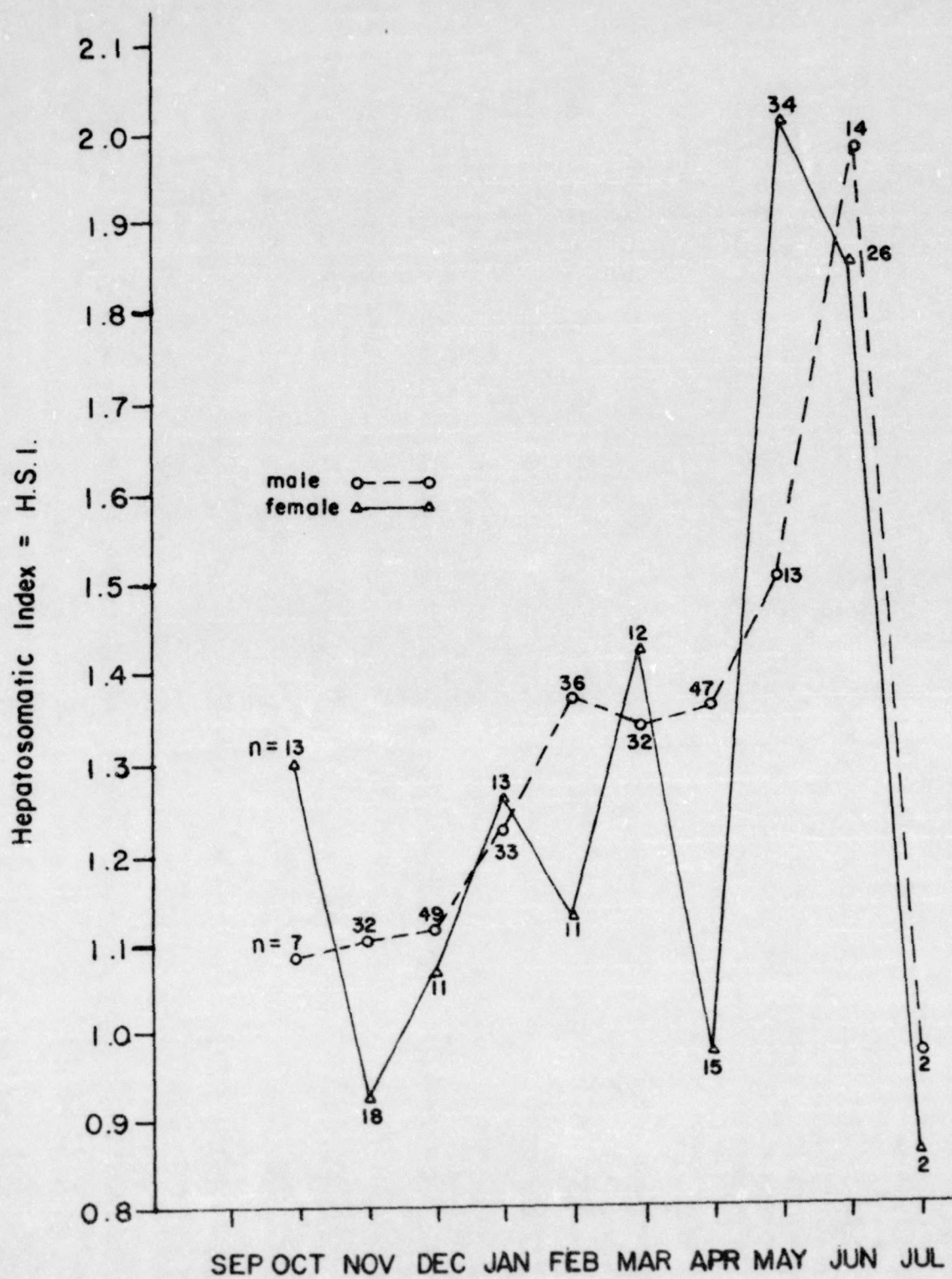
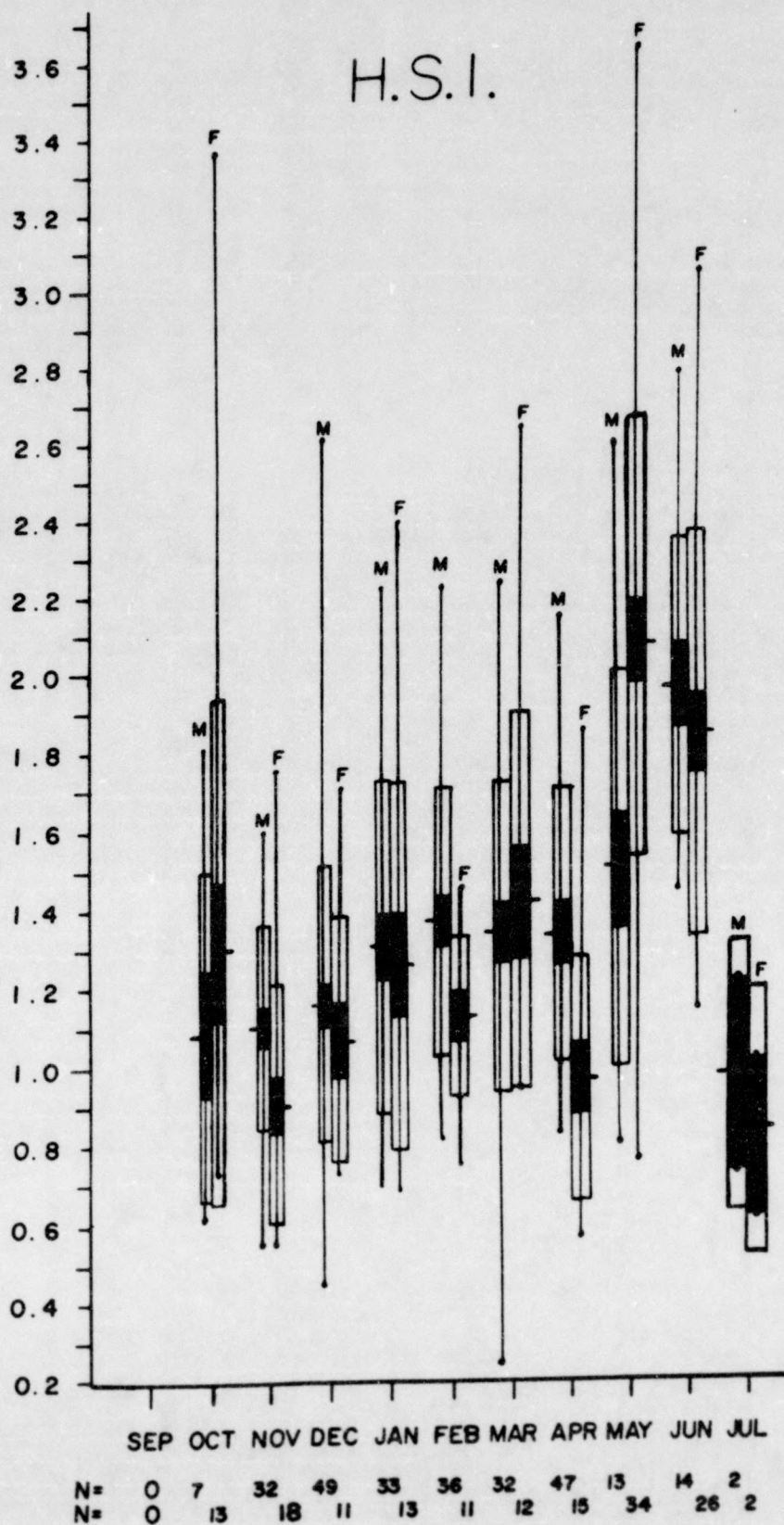


Figure 10. Monthly Hepatosomatic Indices, means, standard deviations, standard error of the mean and ranges for paddlefish collected from Lake Cumberland, Kentucky, September 1983 to July 1984.

HEPATOSOMATIC INDEX = H.S.I.

H.S.I.



values were 1.73 and 2.07, respectively. The highest monthly average throat fat weight for males was observed in June, 25 g, and for females in May, 38 g. Low monthly averages for both sexes occurred in October, 9.5 and 20, for males and females, respectively. Average monthly throat fat indices for both sexes were highest in June, 2.32 and 2.54, and lowest in April, 1.20 and 1.61, for males and females, respectively (Figures 11 and 12).

Seasonal Trends - Average gonad weights for males declined through the study with the highest seasonal average weights occurring in the fall followed by winter, spring, and summer; the highest average female value was observed in the winter followed by the fall, spring, and summer. The relationships between gonad weight and liver, throat fat, and gonad fat body development were determined for the four seasons (Figures 13 and 14). In both sexes in every season, throat fat weight was not significantly affected by changes in the gonad weight; only summer male and spring female fat storage organs showed a slight decline as the gonad weight increased.

Liver weights in males and females from the summer, fall, and winter showed an increase as the gonad weight increased. The liver weight in spring females declined as the gonads increased (Figures 13 and 14).

Gonad fat bodies showed the greatest change in weight as the gonad weights changed, following the same trend observed for liver weights.

Figure 11. Mean monthly Throat Fat Indices for paddlefish collected from Lake Cumberland, Kentucky, September 1983 to 1984.

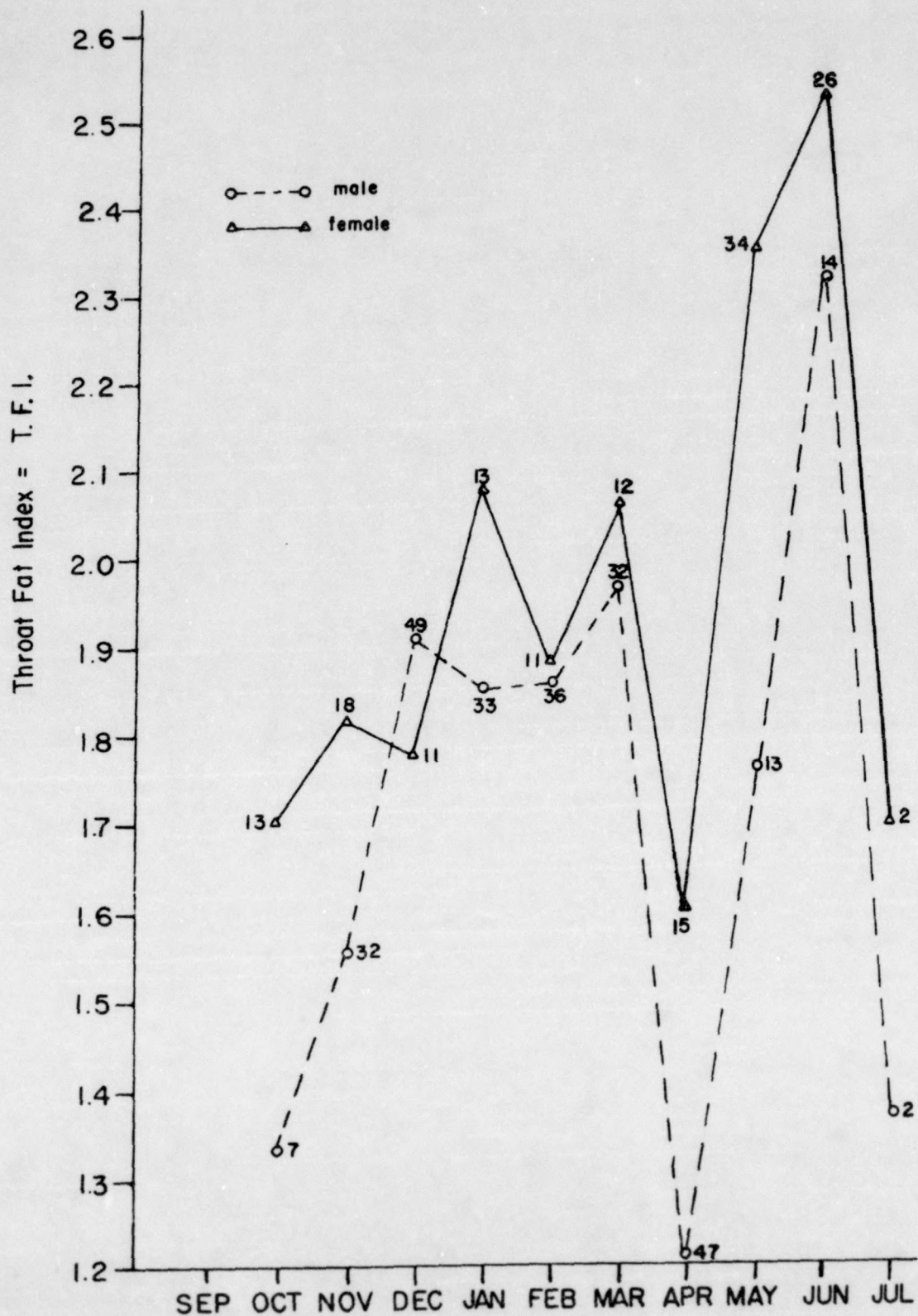


Figure 12. Monthly Throat Fat Indices, means, standard deviations, standard error of the mean, and ranges for paddlefish collected from Lake Cumberland, Kentucky, September 1983 to July 1984.

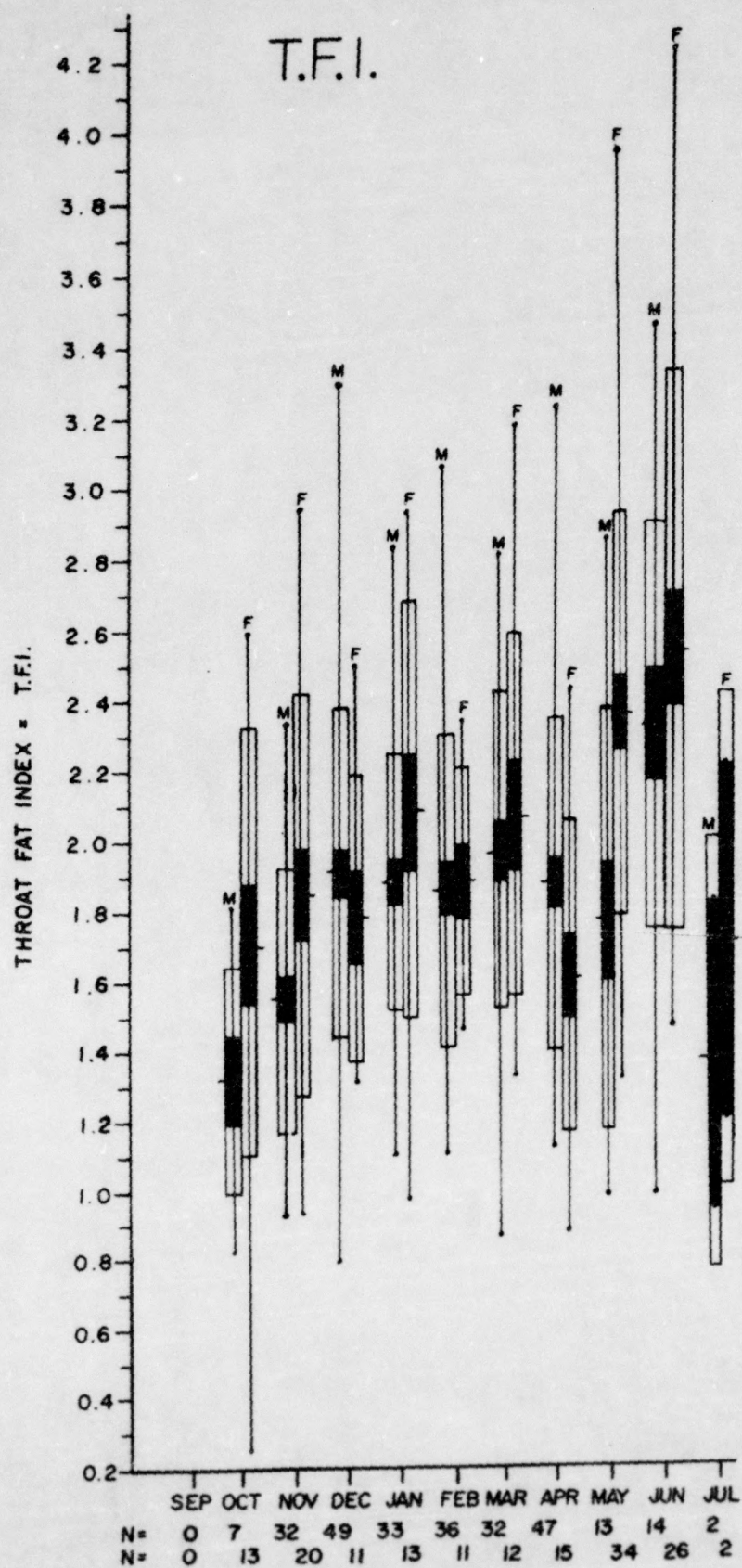


Figure 13. Linear regression and correlation coefficients of fat body weight, liver weight, and throat fat weight on gonad weight, for male paddlefish collected from Lake Cumberland, Kentucky, September 1983 to July 1984.

MALES

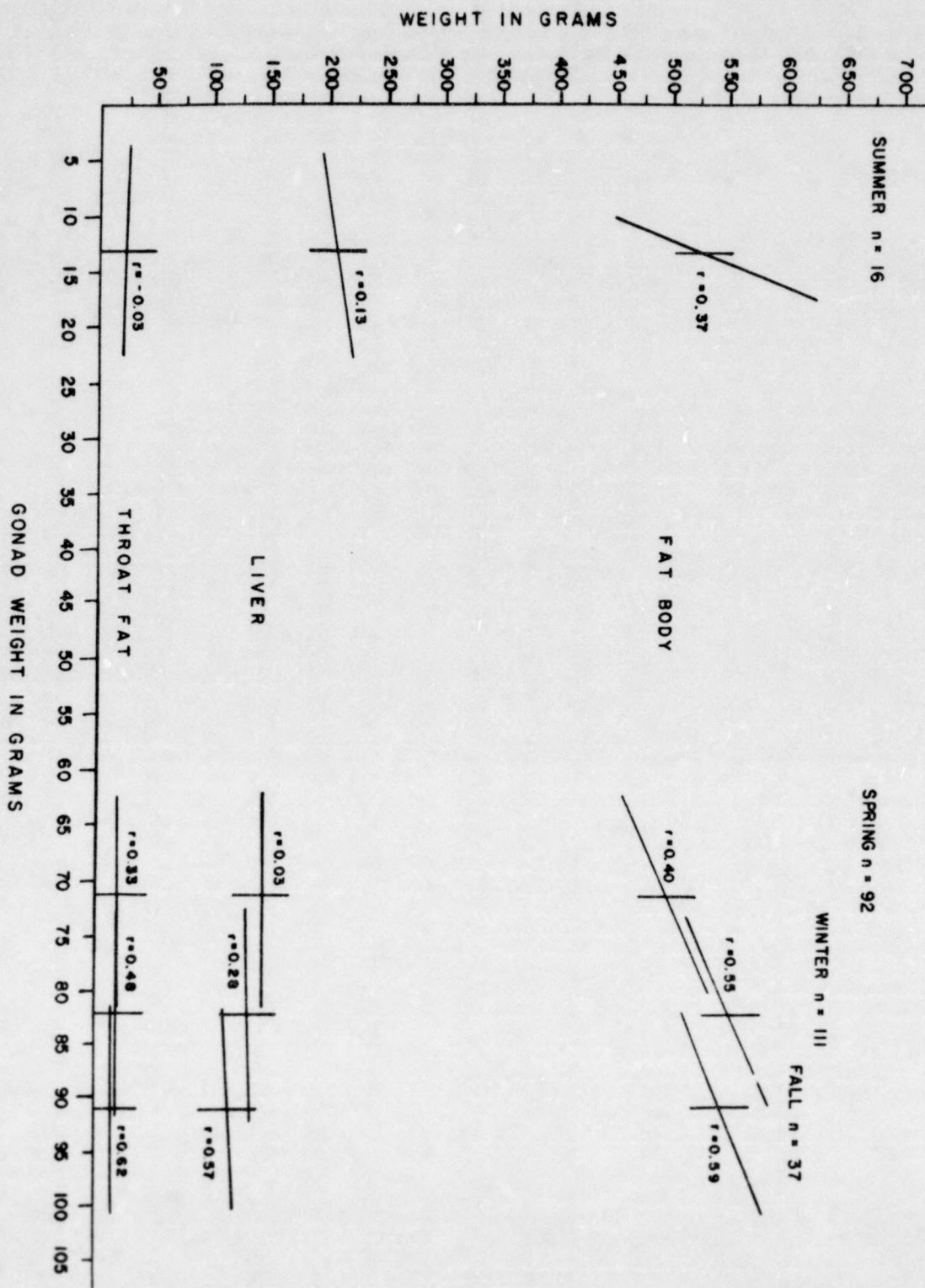
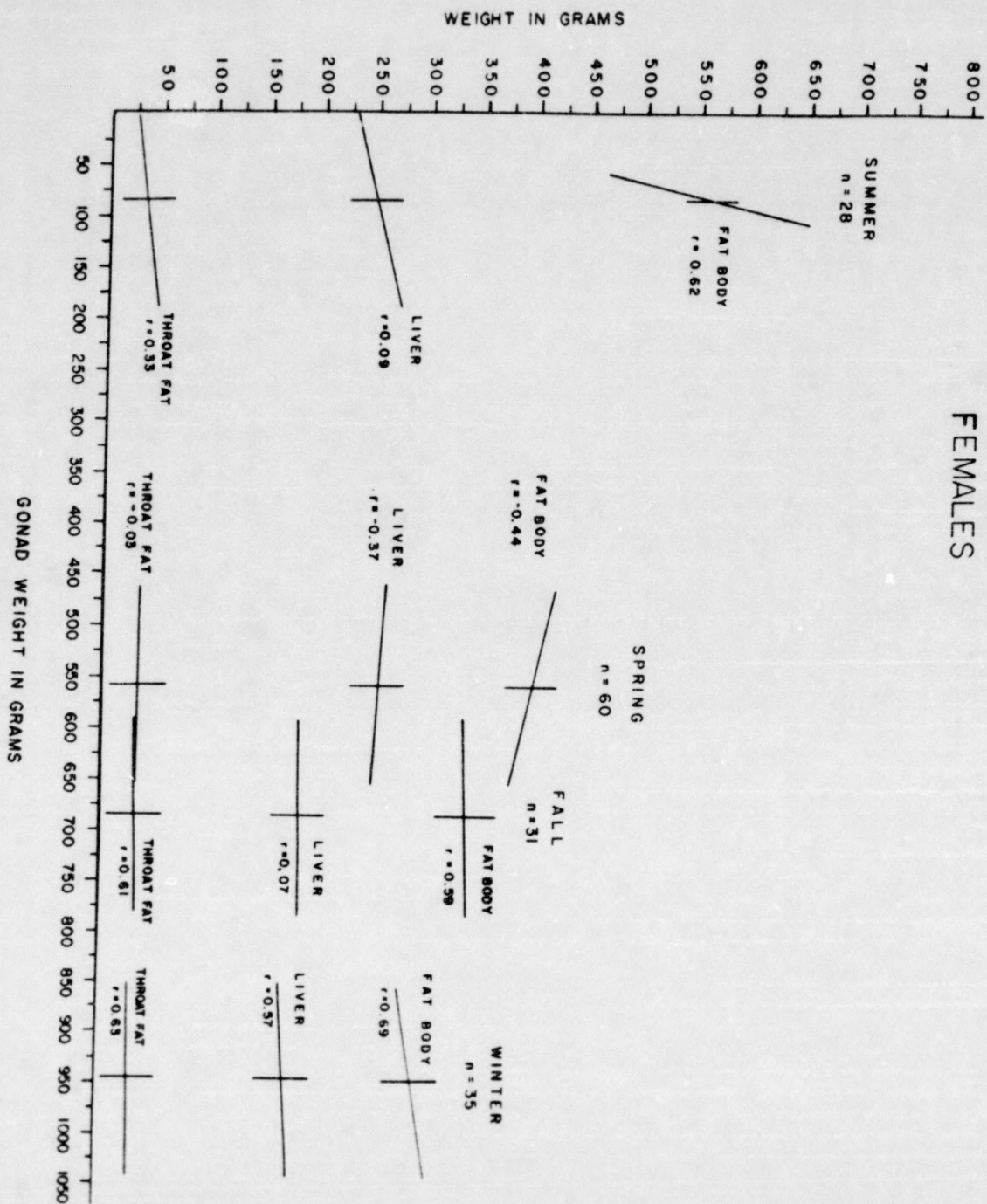


Figure 14. Linear regression and correlation coefficients of fat body weight, liver weight, and throat fat weight on gonad weight, for female paddlefish collected from Lake Cumberland, Kentucky, September 1983 to July 1984.

FEMALES



Maximum reproductive development was observed on specimens captured on April 27-28, 1984 from the Big South Fork. Both males and females exhibited prominent tubercle development, and all fish handled exuded milt or eggs on the nets and in the boat. Of the 16 dead paddlefish collected on this trip, 2 were females and 14 were males. Water temperatures and dissolved oxygen concentration in the stream were 16 C and 9.2 mg/l at the surface and 14 C and 9.4 mg/l at 5 m. At the time of collection the stream was swollen by recent rains and out of the channel bed.

DISCUSSION

Studies of the reproductive biology of the paddlefish are not well represented in the literature. Many studies deal with the artificial propagation of paddlefish (Meyer and Stevenson 1962; Purkett 1963a; Ballard and Needham 1964; Needham 1965; Friberg 1972; Russell 1973; Kallemeyn 1974) and their reproductive ecological requirements (Purkett 1961; Pasch et al. 1980; Wallus 1983; Alexander and Peterson 1983; Hoyt 1984a). Several other studies not directly related to reproduction touch upon it in one aspect or another. Some of these include paddlefish gametogenesis (Larimore 1950), age and growth (Houser 1965), seasonal movements (Southall 1982), and biology and life history (Stockard 1907; Robinson 1966; Gengerke 1978; Combs 1981). No one paper deals exclusively with the reproductive biology-ecology of the species.

Lake Cumberland paddlefish were believed to have spawned during the last two weeks of April and the first two weeks of May in 1983 and 1984. This suggested spawning period was similar to that reported by Stockard (1907), Purkett (1961), Pasch et al. (1980), Wallus (1983), and Alexander and McDonough (1983). Larimore (1950) suggested that, generally, paddlefish spawn as early as March in their southern-most range and in late May in their northern-most

range. The environmental conditions conducive to initiating paddlefish spawning have been reported by Stockard (1907), Purkett (1961; 1963a; 1963b), Friberg (1971), Kallemeyn (1974), Pasch et al. (1980), Rosen et al. (1982), Southall (1982), Alexander and McDonough (1983), Wallus (1983), and Hoyt (1984b) to include water temperatures of 11.5 - 17 C and rapidly rising water levels. Alexander and McDonough (1983) determined a minimum mean daily flow requirement of 275 cubic meters per second for reproduction. Similar conditions were observed in the Big South Fork of the Cumberland River in April and May of 1984 when the water levels rose 8.23 m and water temperatures were 11.75 to 17 C. Spawning habitat was felt to include large submerged boulders and leafy shoreline vegetation.

The onset of reproductive development and spawning activity was accompanied by noticeable changes in the behavior patterns of Lake Cumberland paddlefish. During the winter and spring, the seasons preceding and including spawning, the sex ratio of males to females greatly increased with males representing more than three times the number of females. This concentrating of males around females probably related to insuring that females completed the spawning migration and egg release and increased the percentage of eggs fertilized (Moyle and Cech 1982). An additional explanation for more males than females may be due to males becoming sexually mature earlier than the females, but this may be countered by the females living longer than the males. Sex ratios of spawning paddlefish

have been reported to be as high as 35.9:1 males to females by Robinson (1966). During the remaining two seasons, when reproductive development and activity were minimal, sex ratios of 1:1 were observed. Generally, reported sex ratios favored males throughout the year 54:32 (Helms 1976), 56:51 (Rehwinkel 1978), and 60:40 (Russell et al. 1980). Another behavioral activity attributable to reproductive development and spawning was the traveling of great distances by paddlefish to reach suitable spawning areas. Similar movements have been reported by Stockard (1907), Wagner (1908), Thompson (1934), Purkett (1963b), Robinson (1966), Rehwinkel (1978), Rosen et al. (1982), and Southall (1982).

Two seasonal movements of paddlefish from the lake into upstream tributaries were observed in Lake Cumberland in early fall (September and October) and in the spring (March, April, and May). These movements were complex including moving well upstream into one tributary and then reversing the direction back down to the main lake and up the other major tributary. Similar observations were made during the fall and spring movement periods. These movements were consistent with the onset of reproductive (gonad) development as early as October and were probably stimulated by changing day length and decreasing water temperatures. Maximum movements, however, were observed in the spring during the actual spawning migration when paddlefish proceeded further upstream to the head waters of the Big South Fork Creek and to the foot of the Cumberland Falls on the Cumberland River.

Lake Cumberland paddlefish became sexually mature (V in males and VIII in females) at ages similar to those reported by Adams (1942), Helms (1976), Gengerke (1978), and Combs (1981). However, these ages were lower than those reported by Larimore (1950) and Meyer (1960), possibly a result of the more nearly optimal environmental conditions provided by a lake versus a riverine setting. Stockard (1907), Friberg (1974), Unkenholz (1979), and Rosen et al. (1982) suggested a competitive growth advantage of lake paddlefish over river or stream members of the species due to greater food availability (plankton) in lakes versus rivers. Males reaching sexual maturity earlier than females was expected and has been reported by Friberg (1972), Elser (1973), Russell et al. (1980), and Carlson and Bonislowsky (1981). Sexual maturities were determined by the gonosomatic index, a measure of the amount of energy invested in the production of offspring among fishes that do not provide any parental care (Moyle and Cech 1982). No comparative figures for paddlefish were available in the literature.

Male and female paddlefish in Lake Cumberland exhibited different reproductive histories as illustrated by their participation in annual spawning events. Male specimens, upon reaching sexual maturity, appeared to produce viable gametes annually and participated in every reproductive event thereafter until death. Many if not all, sexually mature females participate in spawning events on an irregular basis, every first and third year, first and fourth year, etc. Similar suggestions have been made for

the species by Houser and Bross (1959), Meyer (1960), Houser (1965), Backlund (1971), and Carlson and Bonislowsky (1981). This conclusion for Lake Cumberland fish was based upon the gonosomatic indices of those sexually mature females in the lake proper being significantly lower than those mature specimens moving into the up-lake tributaries in the fall before the spawn and in the spring. Males did not show this pattern; sexually mature males in the lake proper and up-lake tributaries had essentially the same gonosomatic indices.

Gonadal development in Lake Cumberland paddlefish differed from that of the typical teleostean pattern in that it started as early as September-October of the year before the spawn and continued until egg release, as contrasted to that exhibited by many teleosteans. The observation of the left gonad weighing more than the right organ was referred to by Hoar (1969) as a general phenomenon and was noted in paddlefish by Meyer (1960) and Vasetskiy (1971). Paddlefish gonads, both testes and ovaries, were embedded in well developed fat bodies. In spring females the fat bodies responded inversely with gonad development, decreasing in size as gonads increased, implying an energy source for gonad growth. Larimore (1950) also noted that undeveloped gonads had excessive fat, whereas ripe ovaries were relatively free of fat. The extensive development of paddlefish ovaries sufficient for reproduction (approximately 4.0% of body weight) required the accumulation of additional energy stores in other organs.

This was observed to occur in the liver and fat pads in the antero-dorsal digestive tract wall of the paddlefish. Weisel (1973), in describing the histology of the paddlefish liver, reported liver cells to contain abundant fat deposits. The liver showed the same inverse weight correlation with the gonads as did the fat bodies and was concluded to be important in the energetics of gonad development. Billard and Breton (1978), in working with the brown trout, reported the liver to be the main source of lipid for vitellogenesis, although the liver size does not always appear to be directly connected with specific gonadal events. Weisel (1973) also reported throat fat or esophageal fat rods to be prominent areas of fat deposits. While believed to be involved in the energetics of reproductive metabolism, they did not show a direct size correlation with specific gonadal events.

The extent of energy reserves (Rosen and Hales 1981) or the food reserves stored in body muscle (Htun-Han 1978) can be described with the Coefficient of Condition ("K"). The pattern of "K" values closely corresponded with the development of the gonads as indicated by the gonosomatic indices. Condition values observed for Lake Cumberland paddlefish were higher than those values reported for Missouri River paddlefish (Rosen 1976; Rosen and Hales 1981, 1982; and Rosen et al. 1982). The higher condition values of Lake Cumberland paddlefish over their riverine counterparts again suggested more favorable growth conditions in lake vs. river environments.

Estimated average annual fecundity for Lake Cumberland paddlefish was generally similar to that reported in other studies: 82,397 - 269,043 (Robinson 1966), 241,916 - 506,516 (Helms 1976), 314,000 - 315,000 (Unkenholz 1976), and 148,782 - 506,516 (Gengerke 1978). Variations in the above fecundity estimates were due to low numbers of fish studied, fish being captured at different times of the year, fish representing different environments, estimates being made on intact organs versus estimates made on eggs stripped during artificial propagation projects, and the use of fish of different sizes and ages. Gengerke (1978), using eye-fork length and body weight determined linear regression models for predicting increasing ova numbers as fish increased in size in the Mississippi River. However, no observable relationship was seen between number of eggs and fish size in Lake Cumberland paddlefish.

Ova development in those Lake Cumberland paddlefish participating in the upcoming spawn began early in the fall of the preceding year. Those individuals were observed to have well developed eggs as early as the October before the spawn. Their eggs had reached a size sufficient for use as commercial caviar seven months before spawning. Robinson (1966) reported a similar observation in one Missouri River paddlefish which had mature eggs as early as August.

While no correlation between fish size and egg number was observed in Lake Cumberland paddlefish, ova diameter was found to increase through time, reaching an average maximum diameter of 3.0 mm at the time of egg release. This maximum

average diameter was slightly larger than those diameters reported by Stockard (1907), Larimore (1950), and Robinson (1966).

Those paddlefish undergoing reproductive development, all sexually mature males and some females, exhibited prominent secondary sexual characteristics. Both male and female individuals were observed to exhibit tubercular development, especially on the head and nape of the back. Friberg (1971), however, noted tubercles only on male specimens. Rosen (1976) suggested the presence of tubercles on both sexes and concluded that tubercles alone could not be effectively used to distinguish the sexes. Alexander and Peterson (1982) suggested that if the vent were elastic enough for the easy insertion of the fifth finger and displayed a red swollen appearance, the paddlefish was most likely a female. In this study, all sex determinations were confirmed upon dissection, and it was found that sexually mature male paddlefish were considerably smaller in length and weight than their female counterparts and were more stream lined, having a smaller girth or body diameter, than females. This observation was also made by Rosen (1976) and Rosen et al. (1982). Friberg (1972) and Unkenholz (1979) reported body size and shape, degree of papillae development around the urogenital pore, and tubercles in combination as a means of separating the sexes.

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